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A POTENTIAL SNAIL HOST OF ORIENTAL SCHISTOSOMIASIS IN NORTH AMERICA (POMATIOPSIS LAPIDARIA)

By R. Tucker Abbott

The recent preliminary experimental work of Horace W. Stunkard (1946) has shown that the snail *Pomatiopsis lapidaria* (Say) is capable of serving as intermediate host, at least to the sporocyst stage, of the Oriental human blood fluke, *Schistosoma japonicum* Katsurada. It is possible that further experiments, particularly through the infection of young snails, will prove successful. Malacological studies indicate that this North American snail is strikingly similar to the known Oriental carriers in the genus *Oncomelania;* hence we are holding it at present under suspicion as a potential carrier.

Whether or not, with the accidental introduction of schistosomiasis into this country, this snail would become of medical importance in the future, it seems wise at this time to record what we know of its distribution, habits, and morphology. At present, the danger of an outbreak is remote. The epidemiological conditions in this country are not favorable for the spread of this type of disease, and laboratory infections of the snail are not necessarily a forecast of its activity in the field.

As an aid to public-health workers and parasitologists, we have gathered all the known locality records for this species and spotted the 170 stations on a map (fig. 10). A few records that represent excellent sources of material are given in detail; the other records are on file and available at the Division of Mollusks, United States National Museum, Washington 25, D. C.

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Acknowledgments are due Dr. Henry van der Schalie, who kindly sent living specimens from which dissections were made. The majority of the locality records were sent by Dr. van der Schalie from the world's largest *Pomatiopsis* collection at the Museum of Zoology, University of Michigan. William J. Clench, curator of the department of mollusks, Museum of Comparative Zoology, at Cambridge, Mass., generously made his collection and its facilities available for part of this study. Dissections and bibliographic research were made both at Cambridge and at the division of mollusks at the United States National Museum.

Family AMNICOLIDAE

Subfamily HYDROBIINAE

The genus *Pomatiopsis* Tryon, 1862, is being placed in the family Amnicolidae and the subfamily Hydrobiinae. Various authors in the past have put *Pomatiopsis* in a subfamily and even family of its own. However, in all its characters, animal, shell, and operculum, it is properly a hydrobiine. We believe it should appear alongside the genus *Oncomelania.*

The genus *Pomatiopsis* in North America contains a number of species whose anatomical features have not as yet been investigated and a complete monograph will have to await further study. A catalog of the American species of *Pomatiopsis* is appended at the end of this paper.

POMATIOPSIS LAPIDARIA (Say)

Cyclostoma lapidaria SAY, Journ. Acad. Nat. Sci. Philadelphia, vol. 1, p. 13, 1817 (no locality).

Amnicola (*Pomatiopsis*) *lapidaria* Say, TRYON, Proc. Acad. Nat. Sci. Philadelphia, 1862, p. 451.

Pomatiopsis lapidaria Say, STIMPSON, Smithsonian Misc. Coll., vol. 7, No. 201, pp. 31–36, 1865.

Description of shell.—Adult shell 5 to 8 mm. (about one-fourth inch) in length, elongate-ovate, thin; color a translucent chocolate-brown to light yellowish brown. Nuclear whorls (developed in egg mass) 2 in number, rounded and glassy. Postnuclear whorls (developed after hatching) 4 to 5 in number, well rounded, smooth except for many small axial lines of growth. Suture between whorls well indented. Base of last whorl short, rounded, with a narrow, fairly deep umbilicus. On rare occasions an adult may have a slightly thickened outer lip of the aperture, though usually this aperture lip is thin and sharp. Operculum very thin, transparent, paucispiral, with eccentric nucleus and 2 to 3 whorls. (See pl. 3, figs. 3 and 4.)

The shell of *P. lapidaria* is strikingly similar to *Oncomelania nosophora* (Robson) of Japan and China, differing only in having the whorls more globose and the umbilicus larger and lacking in

most cases the varix or thickening just behind the outer lip of the aperture. The size, color, and texture of the shell, the early whorls, and the operculum are very much the same in appearance.

FIGURE 10.—Map showing distribution of the snail *Pomatiopsis lapidaria* (Say) (solid circles) and the disease it carries, *Paragonimus* (open circles; from Ameel, 1934).

Animal (pl. 3, figs. 1 and 2).—Animal small, with a simple foot, the underside of which is broad and short, rounded behind and truncate in front. Anterior edge of foot with a narrow, deep mucus slit to which may be seen leading a series of short mucus canal ducts. Head relatively small, proboscis or snout blunt, short bilobed in front. Single tentacle on each side of the head simple, slender, swollen at the outer base where the eye is located. In male specimens the verge or penis is located well behind the head on the dorsal side of the body and on the midline. Penis simple, with a single functional sperm duct.

There is considerable variation in its shape among males from the same locality, ranging from a simple, flattened, tapering cylinder to a prong with a "meat-chopper" blade on one side (see pl. 3, fig. 6, *a–d*). Mantle of animal thin, with a slightly thickened border. The gills or ctenidia consist of a series of 27 to 29 low, narrow lamellae or platelike flesh folds attached to the inner side of the mantle.

COLOR: In general a dark blackish gray. The most distinguishing color markings are the bright splotching of yellow or yellowish-white granularlike dots over each eye, forming false "eyebrows." Underside of foot light slate-gray, peppered with minute white dots. Tentacles sandy brown to gray with a clear, colorless rim. Proboscis gray to gray-brown, with a narrow, clear rim on the anterior edge. The penis at its base is dusted with black specks, the remainder being a translucent yellowish gray.

The animal of the species is very similar to *Oncomelania nosophora* (Robson) and *O. hupensis* Gredler. Previous accounts of the divided foot and loping locomotion of *Pomatiopsis* are misleading. When crawling out of water the animals of *Oncomelania* and *Pomatiopsis* have the same type of motion, and both produce folds in the flesh of the foot due to the weight of the shell and body. In *Pomatiopsis* this is accentuated to such a degree that the foot appears divided. When immersed in water the folds disappear and locomotion is accomplished by gliding. The penis in *Oncomelania* is constantly a simple prong, while in *Pomatiopsis* a number of simple variations of this type are expressed in the form of side blades.

The yellow "eyebrows" in *Oncomelania* decrease in size and brightness the farther north the habitat. The yellowest and largest "eyebrows" are found in *O. quadrasi* (Möllendorff) of the Philippines, with those of *O. formosana* (Pilsbry and Hirase) of Formosa, *O. hupensis* of China, and *O. nosophora* of China and Japan becoming progressively whiter and smaller. *Pomatiopsis lapidaria* individuals from one colony express variation from almost no "eyebrow" coloring through distinctly yellow to a whitish yellow. This latter color is fairly common in a colony of living *O. nosophora* examined from Kurume, Chikugo Province, Kyushu Island, Japan.

The reproductive, nervous, and digestive systems of the two genera show few differences. Drawings of the central nervous system of *Pomatiopsis lapidaria* (Say) and *Oncomelania hupensis* Gredler are included. The latter was indaequately figured by Heude in 1882, and since Annandale (1924) attempted to compare it with other *Oncomelania* for systematic purposes, we are recording our findings to show that no significant difference of taxonomic importance can be found between the two genera. The central nervous systems of *Oncomelania quadrasi* figured by Abbott (1945), *O. nosophora* (Robson), and *O. hupensis* are almost identical.

Previously unrecorded in either *Oncomelania* or *Pomatiopsis* is a peculiar modification of the digestive system. Within the stomach is a thin, clear lining (of chitin?), which is crudely shaped into a corkscrew funnel. Flaps extending from the funnel line the walls of the stomach in its lower or posterior half. It has been observed in living and feeding snails that the mixture of food and sand, passing from the esophagus into the stomach, is forced through the center of the funnel, thus grinding the sand particles and food together. The contents swirl around at the rate of about 50 revolutions per minute. Within the lower part of the stomach and partially sheathed by the auxiliary flaps of this gastric sheath is a jellylike, elliptical, crystalline style, which in other mollusks is known to produce digestive enzymes. In *Oncomelania* the gastric sheath and crystalline style are more highly developed than in *Pomatiopsis*. *O. quadrasi* young were observed to pass food through the entire alimentary system in four minutes. While the swirling motion through the stomach continued as long as there was food present, the radula scraped periodically at the rate of 53 revolutions per minute. (See pl. 3, fig. 5.)

Radula.—The lingual ribbon or radula of this species is hardly distinguishable from that found in *Oncomelania hupensis* and *nosophora*. There are 92 to 95 rows of teeth on the ribbon, which is held together by a thin, transparent membrane bearing two side wings. Each row consists of a single rachidian (or central) tooth flanked closely on each side by first a lateral, then an inner marginal and lastly by an outer marginal tooth. Each tooth bears a characteristic number of tiny denticles. Radula counts in this paper refer to the number of denticles on each tooth. *P. lapidaria* from Ann Arbor, Mich., generally had a count of $\frac{1-1-1}{3-3}$; 2–1–3; 7; 5, although the lateral occasionally varied on the same ribbon as 2–1–2 or 2–1–4. Some inner marginals had only 6 denticles. Specimens in Washington, D. C., usually had a rachidian count of $\frac{1-1-1}{2-2}$, although a few ran $\frac{1-1-1}{3-3}$. Many specimens of *Oncomelania hupensis* from Hung-Jao Road, Shanghai, China, have shown these same counts.

Sexual dimorphism.—Population studies on this species have shown a difference in the mean size of males and females. This is not unusual in many dioecious species, and in most of such cases the males are the smaller. The size difference in sexes and the mean size of the entire population vary from colony to colony. The histogram (fig. 11) represents the distribution of the length of adult males and females from one colony. The clear columns of the histogram, denoting males, have been added to the shaded areas denoting females, so that the histogram is a sum of both sexes. This population from Ann Arbor, Mich., produces a well-balanced, normal population curve, but in a colony from Grand Rapids, Mich., the lengths of the two

sexes are sufficiently different to create a bimodal curve, the males being the smaller. The bimodal curve is particularly accentuated in Philippine colonies of *Oncomelania quadrasi*, but almost absent in populations of *O. hupensis* in China. It is known that in certain marine genera, such as *Strombus*, one species characteristically shows sexual dimorphism, while other species in the same genus do not.

No studies have been undertaken to determine what role is played in causing this population variation by such factors as proportion of sexes, population size, availability of food, and distribution of multiple alleles. In the Philippines, where *O. quadrasi* lives in slow-running creeks and where little or no migration of individuals takes place, 0.5 to 1.0 mm. difference in mean length can be obtained from a number of discreet colonies of the same creek system.

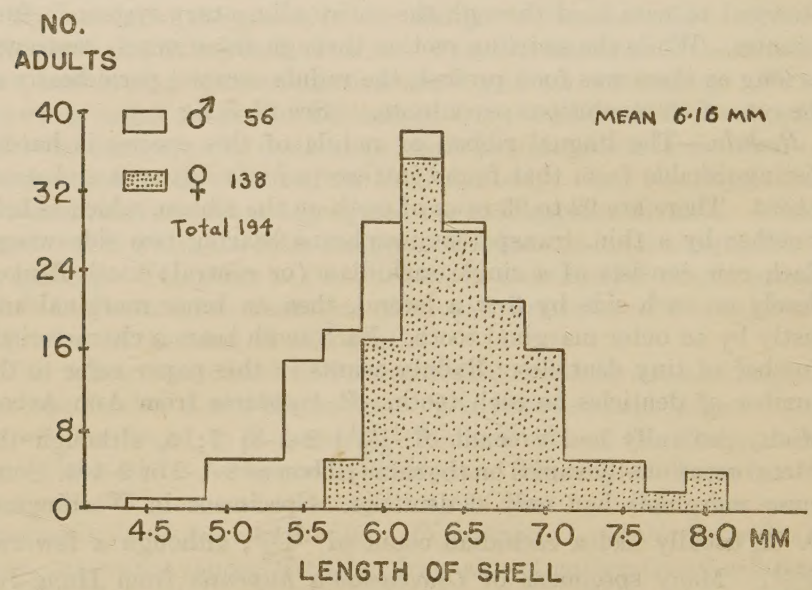

FIGURE 11.—Histogram of the shell length of a colony of adult *Pomatiopsis lapidaria* (Say) from Ann Arbor, Mich. Clear areas, denoting males, are added and not superimposed on shaded areas denoting females.

Habitat and habits.—This fresh-water species is even more amphibious in its habitat preference than *Oncomelania*, although in many respects it could be called the "*Oncomelania*" of North America. Like *Oncomelania*, it spends most of its time out of water in damp vegetation well protected from direct sunlight. When submerged in cool, running water, the animal apparently receives enough oxygen through its gills, and so it makes no attempt to leave the water. The eggs and egg-laying habits of this species are as yet unknown, although they probably lay eggs on moist surfaces at the water's edge as do their relatives, *Oncomelania* (see Abbott, 1946). *P. lapidaria* is slightly nega-

tively phototropic, a condition unknown in *Oncomelania*. Adults can withstand one to two months' desiccation in shade at room temperature.

Pomatiopsis lapidaria occurs in colonies ranging from a few dozen to many thousand individuals. The colonies are usually found sporadically in moist shaded areas near fresh ponds, the banks of stream-cut glens or the overflow lowlands bordering a large river. They are able to tolerate a considerable amount of fine silt from large rivers, an accomplishment not known in *Oncomelania*. Very often colonies increase to noticeable size in the spring, flourish for a few seasons, and then with environmental changes are completely wiped out.

In their more terrestrial habitats their molluscan associates are the nonoperculate land genera *Polygyra*, *Cochlicopa*, *Succinea* (land snails), and *Agriolimax* (land slugs).

Copulation takes place in spring and early in summer. A few weeks later and during most of the summer young appear in the water.

Range.—Minnesota east through southern Ontario to southern New York. South to Alabama and Texas. Eastern Atlantic seaboard from Pennsylvania south to Virginia. No records in New England, the Carolinas, Georgia, or Florida. It has been unable to establish itself on or west of the Great Plains. Known also from loess deposits of the Pleistocene in the Midwest.

Selected locality records (also see map).—CANADA: **Ontario:** Along river bank about one-half mile upstream from bridge at Marsh's Mill, Aux Sables River, Arkona. UNITED STATES: **New York:** On moss and rocks at foot of American Falls, Niagara; Cruger, Duchess County. **Michigan:** Mill Pond, one-quarter mile above Geddes, 4 miles southeast of Ann Arbor. **Alabama:** East side of tributary of Shoal Creek, 8½ miles northeast of Florence, Lauderdale County. **Maryland:** Margin of Susquehanna Flats, Havre de Grace, Harford County. **District of Columbia:** Woodland swamp on south bank of Potomac River, one-quarter mile southeast of Key Bridge; canal near Chain Bridge; Fox Ferry, Potomac River. **Virginia:** On wet rotten logs in swamp, Lanexa, New Kent County. **Pennsylvania:** Monocasy Creek, near Bethlehem, Northampton County. **Wisconsin:** Banks of Suamico River, 4 miles southwest of Suamico, Brown County.

Parasitology.—Pomatiopsis lapidaria (Say) was originally implicated as a first intermediate host of the North American lung fluke, *Paragonimus kellicotti* Ward, by D. J. Ameel in 1932. Other cercariae harbored by this snail are *Cercaria pomatiopsidis* Stimpson, 1865 (redescribed by Ameel in 1939), *Cercaria geddesi* Ameel, 1939, *Cercaria marilli* Ameel, 1939, later shown (Ameel, 1944) to be the larval stage of *Nudacotyle novicia* Barker, and the cercaria of *Euryhelmis monorchis* Ameel, 1938 (Ameel, 1939). Ameel found that adult snails could not be infected experimentally with *Paragonimus* miracidia, but

an infection of almost 100 percent was obtained in young snails of approximately 1 mm. in length. He reports that 78 to 93 days elapse between initial miracidial penetration and cercarial emergence. Cercarial shedding takes place in late afternoon or night. Stunkard (1946) reports that this species will harbor the larval stages of *Schistosoma japonicum* as far as the mature sporocyst stage.

Oncomelania nosophora (Robson) is one of the main intermediate hosts of *Schistosoma japonicum* in China and Japan, but it is also known to serve as host to *Paragonimus westermanii*, a close relative to *P. kellicotti* (Chen, 1941). This may indicate that *Oncomelania* and *Pomatiopsis* have a similar physiological constitution and that *Pomatiopsis* might possibly be capable of serving, at least experimentally, as an intermediate host of *Schistosoma japonicum*. It is well to remember, however, that these two species of *Paragonimus* have not been shown to be the same or distinct species. That one kind of mollusk plays host to a certain trematode does not necessarily mean that the same mollusk will serve as host for a closely related species of trematode. For example, one species of *Schistosoma* is carried by *Oncomelania* (a gill-bearing Streptoneura), another species by *Bulinus* (a lung-bearing Euthyneura). Care must be taken in the use of specificity homologies. Systematic relationships in mollusks are no key to the solution. Of primary importance, however, is the combination of suitable physiological environment and the ideal habitat or external environment of the snail. From this latter standpoint, *Pomatiopsis lapidaria* offers the most suitable conditions in North America for the introduction of *Schistosoma japonicum*.

Our present knowledge of molluscan host specificity is very fragmentary. The final answer will probably come from a physiological analysis of each implicated molluscan species. Miracidia of the trematode must not only be attracted to the snail, but upon entering must develop successfully to the cercarial stages. The miracidia of *Schistosoma japonicum* in the Philippines are not in the least attracted to thiarid or lymnaeid snails, but they do make rapid advances toward *Oncomelania quadrasi* and several species of *Syncera*. *O. quadrasi* is the only known intermediate host of this trematode in that area, but several hundred specimens of *Syncera* examined from the endemic region of Palo, Leyte, showed no signs of infection, nor was an attempt to infect three species of "attractive" *Syncera* successful. Chinese species of *Syncera* collected from the same spot as infected *Oncomelania nosophora* always gave negative results. That miracidia are attracted to *Syncera* is perhaps correlated with the fact that this snail has very much the same amphibious habits as *Oncomelania*. The same commensal ciliates are found abundantly in the mantle cavity of these two genera but are absent from snails that have no attraction for *japonicum* miracidia.

An amphibious nature appears to be a prime requisite of a snail in order to serve successfully as an intermediate host to *Schistosoma japonicum*. The reason for this is still little understood. Whether the nature of the environment, such as periodic fluctuation in the temperature of the snail due to resubmergence in rising and ebbing waters, or a host of other conditions brought about by the external environment, or whether the nature of the physiological environment of the snail itself (conditioned in turn by the external habitat) is what makes this type of snail a suitable host is as yet unknown.

A few scanty observations have been made that aid in defining the habitudinal limits of a schistosome-carrying snail. In the family Amnicolidae there are various genera whose species possess characters that appear to be correlated with a general evolutionary trend toward more and more terrestrial habits. These characters are the number of gills, degree of development of the pedal mucus gland, and the production of mucus. Other characters take a special course in modifications, but their correlation with the trend toward amphibious life is probably accidental.

Genus	*Habitat*	*Number of gills*	*Pedal gland*
*Bulimus*_____	Completely aquatic_____	150–100	Slightly developed.
*Oncomelania*___	Moderately amphibious_	50	Moderately developed.
*Pomatiopsis*____	Distinctly amphibious___	27–28	Well developed.
(Synceridae____	Amphibious to terrestrial	0	Enormously developed.)

Zoogeography.—The distribution of *Pomatiopsis lapidaria* (Say), as indicated on the map (fig. 10), extends throughout the Mississippi River drainage system, into southern Canada, and across into the central portion of the Atlantic Seaboard. The distribution of the lung-fluke disease, *Paragonimus kellicotti* Ward, can be superimposed directly on that of the snail except for the Atlantic seaboard area. The second intermediate crayfish hosts, some ten species of the closely related genera *Cambarus*, *Procambarus*, and *Oroconectes*, have a much wider range than either the first intermediate snail host or the parasitic trematode, and although they are necessary members of the host cycle they do not delimit the distribution of the disease as does the snail.

The origins of the various species of *Pomatiopsis* in North America have not yet been speculated upon, although the close morphological similarity of *P. lapidaria* (Say) and *Oncomelania nosophora* (Robson) suggests that their common ancestor's range extended across the old Bering Sea connection. Some hope may be held for a fairly complete picture of the systematic relationships of the various species of American *Pomatiopsis*, but this will have to come through cytological observation of chromosomal differences, similar to that of Dobzhansky and others with insects. The divergence in external morphology

shown by related forms is not necessarily proportional to the extent of chromosome reconstruction, so that a true picture cannot be obtained from anatomical observations alone.

CATALOG OF AMERICAN POMATIOPSIS

Pomatiopsis binneyi TRYON, Proc. Acad. Nat. Sci. Philadelphia, 1863, p. 148, pl. 1, fig. 10 (Bolinas, Calif.).

Pomatiopsis californica PILSBRY, Nautilus, vol. 12, No. 11, p. 126, 1899 (San Francisco and Oakland, Calif.).

Pomatiopsis chacei PILSBRY, Nautilus, vol. 50, No. 3, p. 84, 1937 (from a swampy place 6 miles up the highway from Klamath, Humboldt County, Calif.).

Pomatiopsis cincinnatiensis (LEA), Proc. Amer. Philos. Soc., vol. 1, p. 289, 1840 (vicinity of Cincinnati, Ohio). (*Cyclostoma.*)

Pomatiopsis hinkleyi PILSBRY, Nautilus, vol. 10, No. 4, p. 37, 1896 (Black Falls, above Florence, Ala.).

Pomatiopsis lapidaria (SAY), Journ. Acad. Nat. Sci. Philadelphia, vol. 1, p. 13, 1817 (no locality). (*Cyclostoma.*)

Pomatiopsis praelonga BROOKS and MACMILLAN, Nautilus, vol. 53, No. 3, p. 96, 1940 (hillside along Elk River, 1.5 miles south of Clay, Clay County, W. Va.).

Pomatiopsis robusta WALKER, Nautilus, vol. 22, No. 9, p. 97, 1908 (Jackson Lake, Wyo.).

Pomatiopsis sayana (ANTHONY), *in* S. S. Haldeman's "A Monograph of the Freshwater Univalve Mollusca of the United States" (no locality printed [Cincinnati, Ohio]). (*Amnicola.*)

Pomatiopsis scalaris F. C. BAKER, Nautilus, vol. 40, No. 4, p. 120, 1927 (New Harmony, Posey County, Ind., in Peorian loess). Pleistocene.

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PLATE 3

Pomatiopsis lapidaria (Say)

1. Side view of animal, × 9. (*p*=penis or verge; *eb*=yellow dermal chromatophores, or "eyebrows.")
2. Dorsal view of animal, × 10. (*md*=mucus ducts of pedal gland.)
3. Operculum, × 10. (*ms*=scar of muscle attachment.)
4. Shell, × 12.
5. Gastric sheath, × 25. Arrow indicates path of food through stomach.
6. *a*, Penis of immature male; *b-d*, variations in penis of mature males. × 12.
7. Gross anatomy of male reproductive system, × 12. (*di*=digestive gland; *pr*=prostate gland; *sd*, sperm duct; *st*, stomach; *te*, testes.)
8. Dorsal view of one row of the radula (slightly spread).
9. End view of radula (slightly spread).

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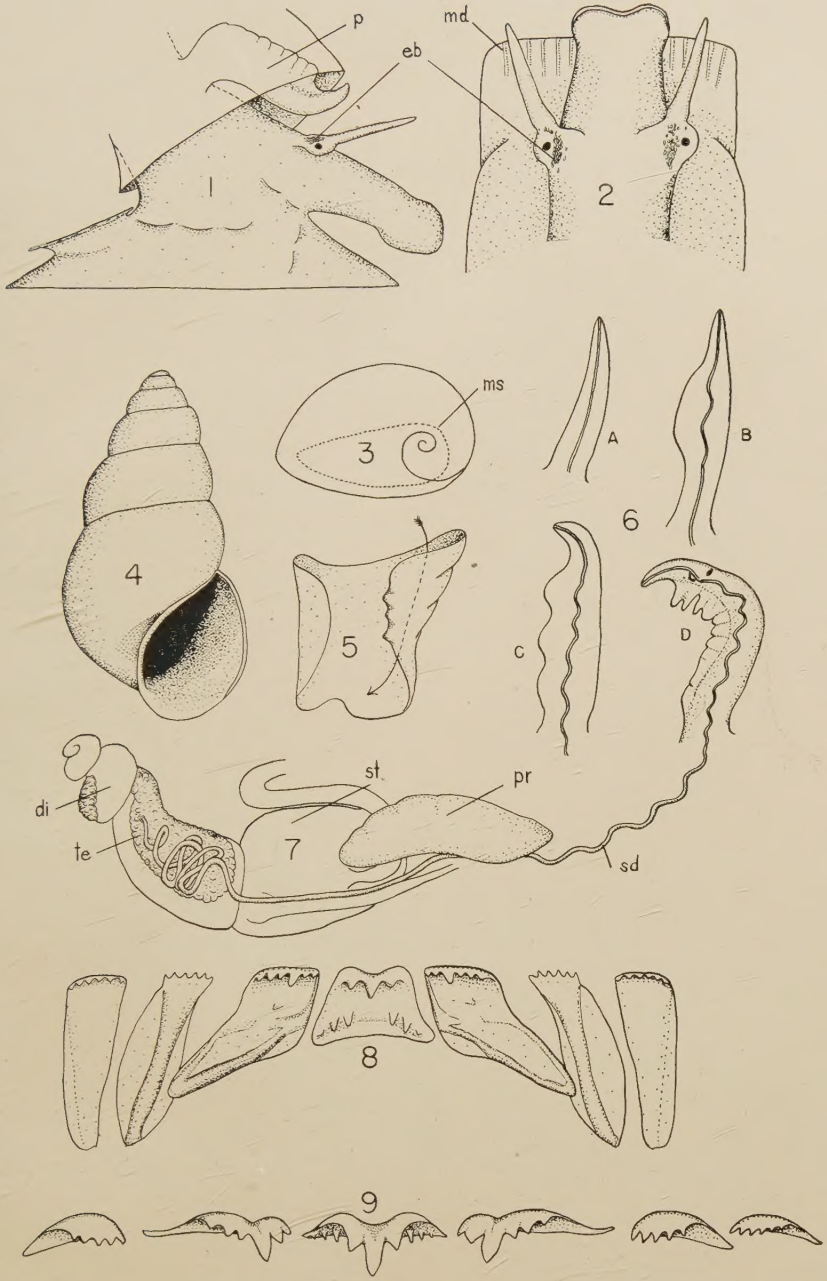

POMATIOPSIS LAPIDARIA (SAY)

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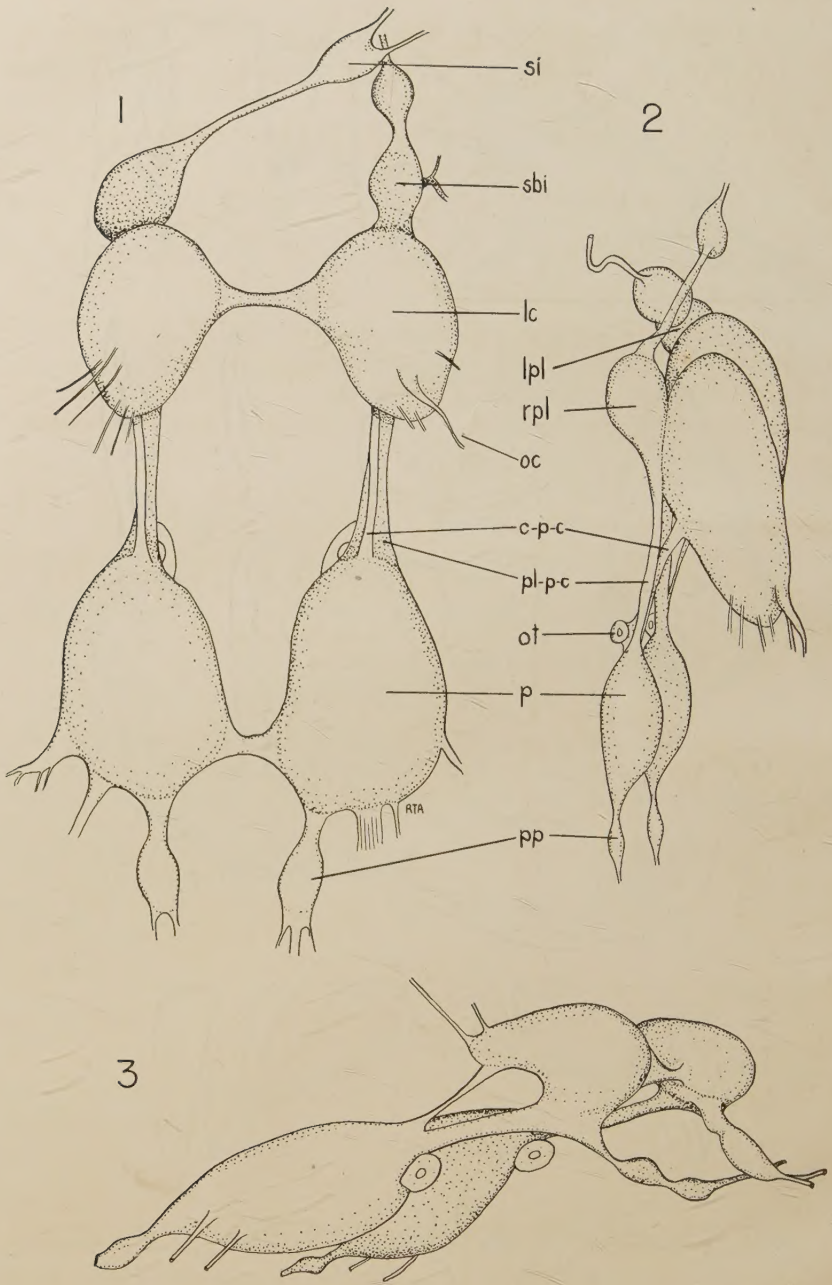

1. Dorsal view of central nervous system of *Oncomelania hupensis* Gredler, × 30.
2. Right side view of central nervous system of *Pomatiopsis lapidaria* Say, × 25.
3. Three-quarters view of central nervous system of *Oncomelania hupensis* Gredler, × 25.

[*c-p-c*=cerebro-pedal connective; *lc*=cerebral ganglion; *lpl*=left pleural ganglion; *oc*=ocular nerve; *ot*=otocyst; *p*=pedal ganglion; *pl-p-c*=pleural pedal connective; *pp*=parapodial ganglion; *sbi*=subintestinal ganglion; *si*=supra-intestinal ganglion.]